

A dark-morph Sharp-shinned Hawk in California, with comments on dichromatism in raptors

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On 12 November 1994 at 10.30 hrs, Wilson studied and photographed an unusual dark raptor in Hart Park, Bakersfield, Kern County, California. The bird was an obvious *Accipiter* in general shape, but it was mottled chocolate brown on the underparts. An examination of photographs (Fig. 1) and of the written description suggested that it was a dark-morph Sharp-shinned Hawk *Accipiter striatus*. Wilson's notes were as follows:

An odd *Accipiter* perched in a horizontal branch of a bare cottonwood (*Populus* sp.) bordering the north side of the Kern River. The sky was clear, except for slight haze; there was no wind. Initial distance to the bird was about 100 m, but it was eventually approached to within 40 m. Viewed through 8 × 42 Bausch and Lomb Elite binoculars and photographed with a Nikon N8008 camera with a Nikon 300 mm lens and 2 × teleconverter. The bird was observed in excellent light for 20 min.

Size was difficult to judge, but the round-headed appearance, relatively squared tail, and thin tarsi suggested Sharp-shinned Hawk. The overall color of underparts was dark chocolate brown. The breast and belly were somewhat mottled with a darker brownish. The thighs, cap, nape, and wings were a darker brown. The underside of the tail appeared to be somewhat striated with a wide dark brown tip and at least two visible cream-colored bands about half the width of the terminal band, with each bordered by a thin dark brown band. The iris was yellow, similar in color to that of an immature Sharp-shinned Hawk. There were short golden-yellow supercilia extending



Figure 1. Dark-morph Sharp-shinned Hawk *Accipiter striatus* at Hart Park in Bakersfield, California, U.S.A., 12 November 1994. Photograph by John C. Wilson.

from just in front of the eyes to an equal distance behind the eyes. The supercilia were bordered inferiorly by a thin dark brown line. The cere was pale yellow. The legs and feet were bright yellow.

During its stay on the perch this bird was studied by David G. Yee as well, including views through a Kowa telescope at $30\times$ for 10 min. The bird eventually dropped to the ground, at which point a few pale (perhaps even whitish) feathers were noted on the back. The bird remained on the ground for 20 min, such that observation time totaled nearly one hour.

Dark morphs are known in some South American populations of Sharp-shinned Hawk, such as *A. s. ventralis* (Blake 1977, Hilty & Brown 1986, Palmer 1988; del Hoyo *et al.* 1994 consider *ventralis* to be specifically distinct). However, dark morphs are not known in *A. s. velox*, the widespread North American subspecies, nor in *A. s. perobscurus*, the subspecies found on the Queen Charlotte Islands (Clark & Wheeler 1987). Whereas *perobscurus* has decidedly darker underparts than *velox* (Friedmann 1950), both of these subspecies show an underpart pattern very different from that shown by the Bakersfield bird: rather than being essentially uniform brown below, immatures of these subspecies show varying degrees of heavy brown streaking and/or mottling on whitish underparts. The description and photographs argue against this bird being *ventralis* (i.e. it is not clear, rufous-brown below) or being a darker individual of *perobscurus* (i.e. it is well outside the known range of variation for that subspecies). A positive racial determination cannot be made without a specimen; nevertheless, we believe it most parsimonious to conclude that the Bakersfield Sharp-shinned Hawk represents the first documented dark-morph *A. s. velox*, rather than either a dark *A. s. ventralis* thousands of miles from its home or California's first record of *A. s. perobscurus*.

Dichromatism (and polychromatism) is prevalent in numerous taxa, including birds (Huxley 1955, Paulson 1973). Presumably, dark-morph individuals arise in a population via melanistic mutations. If a selective advantage is conferred on these individuals, through crypticity or frequency-dependent selection for example, then assuming all other things are equal, the prominence of dark-morph individuals should increase in a population. If a particular morph has an advantage that morph would become the most abundant in a population at the exclusion or near-exclusion of the disadvantaged morph, as in the classic example of peppered moths (*Biston betularia*) in Britain (see Ridley 1993).

The frequency and persistence of dichromatism in groups such as raptors is therefore puzzling. Whereas dichromatism is prevalent in *Buteo*, for example, it is absent or scarce in other genera. Some genera show dichromatism only in certain species or subspecies, as is the case with *Accipiter*, a genus in which only eight of the 45–50 species show dichromatism (del Hoyo *et al.* 1994). Another example is provided by the harriers *Circus* spp.: some populations of *Circus* are highly dichromatic, but there is only one record of a dark-morph Northern Harrier *Circus cyaneus* for North America (Howell *et al.* 1992). Light-morph individuals prevail in most species and subspecies of raptors (including *Accipiter*), but in some instances a subspecies or population comes to be dominated by dark-morph individuals, as is the case with "Harlan's" Hawk *Buteo jamaicensis harlani* (Mindell 1983).

One mechanism whereby polymorphism is maintained in a population is via apostatic selection (Clarke 1962, Endler 1991). Unlike in the peppered moth example, where a selective advantage is conferred on individuals with cryptic coloration, apostatic selection is "frequency dependent selection in which a predator selects the most abundant morph in a polymorphic population resulting in a balanced polymorphism" (Lincoln *et al.* 1982). Thus, a "given phenotype is favored in direct proportion to its rarity through frequency-dependent predator pressure" (Paulson 1973). Apostatic selection, therefore, is selection exerted by predators against the more *common* morph of a given prey species.

The definition of apostatic selection was broadened by Payne (1967) to be "selection of individuals which contrast in appearance [with each other] within a population". He further suggested that apostatic selection could be effected *on* predators *by* prey, thus altering the predator-driven definition originally proposed. Paulson (1973) extended Payne's redefinition by presenting the "avoidance-image hypothesis", which predicts that balanced polymorphism will prevail if prey exert selection pressure via avoidance of familiar predator forms. Both Payne and Paulson treated avoidance-image as apostatic selection, but because the avoidance-image hypothesis predicts predator selection by prey, it is in this respect antithetical to the classic definition of apostatic selection. Thus, the term "counterapostatic selection" may be more appropriate for the avoidance-image hypothesis.

In any event, the avoidance-image hypothesis requires avoidance-learning of familiar colours by prey and frequency-dependent selection, both of which have been demonstrated in wild populations (e.g. Hori 1993, Craig 1994); thus, the hypothesis seems plausible. A rare predator morph would have higher fitness by virtue of its rarity so that, all other things being equal, this rare phenotype would increase to commonness in a population (assuming phenotypic expression is heritable, as it is in raptor dichromatism; Paulson 1973). However, such increases have not been documented in a natural population of raptors, as light-morph individuals predominate in most wild populations. Dark-morph individuals seem to be maintained in a population through balanced polymorphism, but they seldom increase to commonness. Nevertheless, there exists empirical evidence that appears to support the avoidance-image hypothesis, suggesting that counterapostatic selection is a valid mechanism for the maintenance of dichromatism in raptors and other predatory birds (Paulson 1973, Arnason 1978, Furness & Furness 1980; *cf.* Rohwer 1983).

However, if one assumes a selective advantage for dichromatic predators, counterapostatic selection seems not to provide an answer for the general lack of dark-morph *Accipiters*. Indeed, because *Accipiters* tend to inhabit forested areas, dark coloration would logically seem to provide a selective advantage by reducing plumage contrast. However, species in this genus feed primarily by surprise attack on ground-feeding mammals and birds (Bielefeldt *et al.* 1992). Because of this foraging behaviour, we believe that counterapostatic selection would exert little influence on dichromatism within this genus. Instead, we suggest that dichromatism is rare in *Accipiters* because the

contrasting plumage of light-morph individuals assists them in prey capture. For certain predators, conspicuous coloration may enhance prey capture by stirring up a flock or causing movement in alarmed prey species (Wilson *et al.* 1988). It would be an advantage to have more contrasting plumage because prey species would flee or flush more readily from a conspicuous predator, providing a more readily visible target. Thus, given the hunting behaviour of *Accipiters*, it is advantageous to be conspicuous, and dichromatism in *Accipiters* is likely to remain rare.

Alternatively, the lack of dichromatism in *Accipiter* may be a result of high capture efficiency, a hypothesis suggested by Rohwer (1983) to explain the lack of dichromatism in the Peregrine Falcon *Falco peregrinus*. This hypothesis states that predators that are extremely efficient are not selected to be polychromatic because they do not benefit from the potential advantage afforded by polychromatism. Not only is this hypothesis invalid for *Accipiter* because its foraging behaviour likely does not favour such selection, it need not be invoked for Peregrine Falcon either, as this is a species that feeds mainly by aerial diving, and pale underparts may be an advantage by enhancing camouflage (Cowan 1972, Götmark 1987). Thus, we would not expect counterapostatic selection to affect this species. Conversely, *Buteos* hunt mainly by soaring, and are thus readily visible, providing a perfect scenario for counterapostatic selection to be effective.

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IN BRIEF

THE CORRECT CITATION OF THE BLUE-CHINNED SAPPHIRE *CHLORESTES NOTATUS*

The name of this bird was accredited in Peters (1945) to "C. Reichenbach 1795", and this appears to have been followed, e.g. by Meyer de Schauensee (1966). However, C. Reichenbach did not exist. Until 1908, this species was generally cited as *Chlorestes caeruleus* (Vieillot), i.e. *Trochilus caeruleus* Vieillot 1817 (vol. 7, p. 361), though in fact the earliest use of this name appears to be Audebert & Vieillot 1802 (vol. 1, p. 40). Berlepsch (1908, p. 266 footnote), apparently on the basis of a letter from C. W. Richmond to Ernst Hartert, pointed out that this name was predated by *notatus*. The first reference in literature to the species appears to be "No. 48 *Trochilus* . . ." Richard & Bernard (1792, p. 117). On this was based *Trochilus notatus* G.C. Reich (1793). Berlepsch used this, the earliest name, but quoted the date as 1795. This date was repeated by Peters (1945) who also made the error of transliterating Reich as Reichenbach. I have examined a microfilm copy of Reich's rare paper, and confirm the name and that the date there quoted is 1793. There is no reason to suppose that this date is incorrect, and if Berlepsch had reason to believe that the date of publication was actually later than the date cited, he would probably have commented. It seems likely, therefore, that the date 1795 is a misprint. The correct citation of *Chlorestes notatus* should therefore be: G. C. Reich, 1793, *Magazin des Thierreichs* (Erlangen) 1, Abth. 3, p. 129. Based on Richard & Bernard 1792, *Cat. Ois. env. de Cayenne à la Soc. par M. le Blond*, in *Actes Soc. Hist. Nat. Paris*, i, 1: 117.